Generalized affiliation indices extract affiliations from social network data

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Abstract

1. In the analysis of animal social networks, a common challenge has been distinguishing affiliations—active preferences of pairs of individuals to interact or associate with one another—from other, structural, causes of association or interaction. Such structural factors can include patterns of use of the habitat in time and space, gregariousness, and differential association rates among age/sex classes.

2. In an approach with similarities to the multiple regression quadratic assignment procedures test, we suggest calculating generalized affiliation indices as the residuals from a regression of the measures of association or interaction on structural predictor variables, such as gregariousness and spatiotemporal overlap. If the original data are association indices or counts of interactions, then generalized linear models with binomial or Poisson error structures, respectively, can be used in place of linear regression. Anscombe or deviance residuals can be used to assess the significance of particular affiliation indices.

3. Generalized affiliation indices can be used as the weights of links in a social network representation. They can then be portrayed in network diagrams or cluster diagrams, and used to calculate network statistics, to delineate communities by maximizing modularity, and to test for overall affiliation using data-stream permutation tests.

4. We evaluate the effectiveness of such generalized affiliation indices using simulated and real association data, finding that the method removes much of the effect of structural variables on association patterns, revealing real affiliations. While the approach is very promising, it is limited by the extent to which the input predictor variables represent important structural factors.

37 Keywords: Social structure; association; interaction; regression; residuals; multiple regression quadratic
38 assignment procedure; permutation test

Introduction

Among the potential goals of social network analysis, perhaps most fundamental is the description and investigation of preferred and avoided dyadic relationships, what we will call affiliations. A frequent objective of social network analysis has been testing the null hypothesis that there are no such affiliations in the study population, and, if this is rejected, identifying dyads with preferred or avoided relationships (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011).

Many, perhaps most, studies of the social networks of non-humans are built upon matrices of association indices, estimates of the proportion of time that pairs of individuals are associated (Whitehead 2008). In this approach, association should be defined such that is meaningful to the animals—how they interact and/or communicate—, but operationally association is usually based upon spatial, temporal, and/or behavioural metrics (Whitehead 2008). Using this approach, pairs of individuals may be delineated as associated if they are 1) communicating/interacting and making active decisions to associate with one another, 2) if they happen to be in the same place at the same time and so communicate/interact, or 3) if they happen to be in the same place at the same time and are not communicating or interacting. If interest is in disease transmission over the social network then all three of these forms of association are important. Forms 1) and 2), but not 3), allow for the transmission of cultural information transmitted through interactions or communication. However if we are interested in actively-maintained dyadic relationships, affiliation, only form 1) is relevant. In addition to true affiliation, factors that might affect association include spatial overlap (animals using the same parts of the population range associate more (e.g. Shizuka *et al.* 2014)), temporal overlap (animals using the study area at the same time are more likely to associate (e.g. Cantor *et al.* 2012)), gregariousness (animals that preferentially are found in large groups are more likely to associate with one another (Godde *et al.* 2013)), and gender (there may be preferential associations with the same or

62 the opposite sex). We shall refer collectively to such sources of association, which potentially mask the
63 existence and strength of true affiliations, as structural variables.

64 Sometimes it is not clear whether a factor should be considered a structural factor predicting association
65 or an element of affiliation. For instance, kinship could be deemed a structural factor if there is a
66 preference to associate with kin, but kinship recognition is not linked to individual identification. If, on
67 the other hand, kinship is perceived by the animals at an individual level ("One of the reasons I like X is
68 because she is kin"), so affecting affiliation rather than association directly, then it might not be
69 considered structural.

70 Disentangling true affiliations from other causes of association has led to the construction of structured
71 permutation tests (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011; Whitehead 1999; Whitehead,
72 Bejder & Ottensmeyer 2005). However such tests have limitations and challenges. They only give a
73 perspective on the null hypothesis that there are no affiliations, or, in the case of a dyadic test (Bejder,
74 Fletcher & Bräger 1998) that two animals are not affiliates. Furthermore as more structural factors that
75 might cause association are accounted for, the tests become increasingly unwieldy. Additionally,
76 network diagrams and network statistics include the non-affiliative causes of association, and so will be
77 misleading if the primary goal is to study patterns of affiliation.

78 An alternative perspective pioneered by Godde et al. (2013) in the case of gregariousness is to correct
79 the association index for the structural factor, and then carry out additional analyses—tests, diagrams
80 and network statistics—on this new index. Here we extend this approach to include multiple structural
81 factors, using a method closely allied with MRQAP (multiple regression quadratic assignment
82 procedures).

83 MRQAP is itself an extension of the Mantel (1967) test in which the non-diagonal elements of two
84 square matrices both indexed by the same objects (usually individuals in social network analysis) for

both rows and columns are tested for a linear relationship. So we might test whether there is an overall correlation between association indices of dyads and their genetic relatedness. Because of non-independence caused by the structure of the data, standard tests of correlation coefficients are invalid, but permutations of the object labels on one of the matrices allows a null hypothesis of no relationship to be tested. MRQAP extends this approach to situations in which the relationship between one dependent variable—typically an association index in social network analyses of animals—and an independent variable—such as kinship—is examined while controlling for other independent variables—such as range overlap or gender similarity. Because of potential collinearity among the independent variables, this is not as straightforward as in the case of the bivariate Mantel test. However, there are effective permutation methods for MRQAP tests (Dekker, Krackhardt & Snijders 2007).

Here we propose that the residuals following a multiple regression of the association index on various structural variables using generalized linear models, be used as generalized indices of affiliation among pairs of individuals. We consider possible structural variables that might be included as predictors of association, how to measure the significance of structural variables, and, having removed the structural factors, how to test for the presence of affiliation both at the dyadic level and globally. We illustrate the method using simulated and real data.

Methods

Calculating generalized affiliation indices

We start with a square matrix representing associations or interactions between individuals. This will often be a matrix of association indices, such as the simple ratio index (Ginsberg & Young 1992), which estimates the proportion of time members of a dyads are associated:

$$y(simple\ ratio)_{ij} = \frac{\text{No. sampling periods } i \text{ and } j \text{ associated}}{\text{No. sampling periods } i \text{ or } j \text{ or both observed}} \quad (1)$$

where y_{ij} is the simple ratio association index between individuals *i* and *j*, given definitions of "association" (e.g. seen within 3 body lengths of one another) and "sampling period" (e.g. hour). Also frequently used is the half weight index in which the denominator of the simple ratio index is replaced by half the sum of the sampling periods in which each individual was observed. However the matrix could list counts of, say, touches between individuals, and it could be asymmetric.

If the non-diagonal elements of the association matrix are listed in an *n*-element vector *Y* (if asymmetric all non-diagonal values are entered and *n* is twice the number of dyads; if symmetric only the upper or lower triangle is needed and *n* is the number of dyads), and the corresponding elements of *v* structural predictor variables for each dyad are given in the *n*-by-*v* matrix ***X***, the generalized linear model is:

$$f(Y) = \alpha X + E \qquad (2)$$

where *f* is a link function, α is a vector of the regression coefficients, and *E* an *n*-element vector of residuals. Following the regression, *E* is then recast as a square matrix in which the *ij* element gives the generalized affiliation index, e_{ij}, between individuals *i* and *j*. A high positive value of e_{ij} suggests affiliation—i.e. that the dyad are more associated than expected given the structural predictor variables—and a negative value indicates avoidance.

If the elements of *Y* are simple counts of interactions—as may be appropriate with small populations when all interactions can be observed—then a Poisson generalized linear model, with a log link function can be used. If an association index (e.g. equation 1), the numerator and denominator of the index can, with the assumption of independence, be considered to be from the binomial distribution. Hence we can use a binomial version of the generalized linear model and a logit link function, with the vector *Y* in equation 2 becoming a *n*-by-2 matrix giving the numerator and denominator of each association index. This formulation is useful in that it corrects for variable amounts of effort directed towards different dyads.

If using a linear model then the residuals from the regression model can be used straight as affiliation indices. When using a binomial model, they should be divided by the denominator of the original association index (as in the denominator of equation 1). With a Poisson model the straight residuals seem to work reasonably (see Results).

We can transform the residuals, for instance into Anscombe residuals or deviance residuals (Pierce & Schafer 1986), which should be distributed as the standard normal distribution. These indicate the statistical significance of particularly large positive or negative affiliations. In our evaluations of real and simulated data (see below), we found that Anscombe and deviance residuals were very similar to one another.

Structural variables and their significance

Structural variables may be continuous, ordinal, categorical, or binary. Here are some that might be employed:

Range overlap: Concurrent use of space is necessary for association or interaction. Thus range overlap (within the study area) will often be a structural variable of concern. Utilization distributions describe how animals use habitat, the probability that they are in a particular place, and can be estimated from real locational data in a variety of ways. Getz et al. (2007) recommend the local convex hull nonparametric kernel method, and its variants, as being superior to other current techniques. We are interested in the extent to which the utilization distributions of different individuals overlap, for which there are several potential statistics, including the utilization distribution overlap index and Bhattacharyya's affinity (Fieberg & Kochanny 2005). These could be appropriate measures of range overlap.

Temporal overlap: Animals may move into and out of the study area where association is observed, and can only be observed associating when they are both inside it. Short time scale temporal overlap, i.e. at

153 a scale similar to the sampling period being used, might be considered an element of affiliation—
154 animals choosing, or not, to be together. Longer time scale emigration/immigration, or birth/death, is
155 perhaps more of a structural factor affecting association. A suitable measure might be an association
156 index, as in equation 1, but using a long sampling period, say a month or year, and defining association
157 broadly as both individuals identified, not necessarily associated, in that sampling period. This gives an
158 estimate of the proportion of time that two individuals were both in the study area during the research.
159 In some cases, such as when data are collected non-continuously in several study locations that are
160 small relative to the ranging patterns of the animals, spatial and temporal overlap might be covered by
161 one predictor variable, similar to the temporal predictor just proposed.

162 *Gregariousness:* Godde et al. (2013) correct standard association indices for gregariousness using the
163 expected values of the association index for a pair, given the estimated gregariousness of each. We
164 could use this as a measure of mutual gregariousness, and a structural variable in the estimation of
165 affiliation:

166 $$x(gregariousness)_{ij} = \frac{\sum_k y_{ik} \cdot \sum_k y_{jk}}{\sum_k \sum_l y_{kl}} \quad (3)$$

167 where y_{ij} is the association index between individuals *i* and *j*, and y_{kk} is set to zero for all *k*. As we are
168 supposing that the association indices may depend on structural factors, including gregariousness itself,
169 this formulation is somewhat circular: a high value of an association index between two individuals
170 increases their joint gregariousness. To remove this effect, we propose removing each dyadic
171 association index when calculating the joint gregariousness of that particular dyad:

172 $$x(gregariousness)_{ij} = Log\left(\sum_{k \neq i,j} y_{ik} \cdot \sum_{k \neq i,j} y_{jk}\right) \quad (4)$$

173 *Gender/ class similarity:* The simplest version of a gender similarity structural variable is: $x(gender)_{ij}$=1 if *i*
174 and *j* are the same gender; $x(gender)_{ij}$=0 if of different gender. This implies that in gender relationships

same and different are the primary factors. Alternatively a categorical variable, with three values, ($x(gender)_{ij}$=MM, MF, or FF) can be defined giving different possible association rates for males with males and females with females, as well as between the sexes. If the population is delineated into other classes that might affect association, for instance age classes, reproductive status or classes based upon mitochondrial haplotypes or characteristic behaviour, then structural variables can be defined in a similar manner.

Social unit membership: If animals are allocated to social units we can use these units as classes to define a structural variable. One possibility is a simple binary same/different unit categorization. A more nuanced categorization, using up more degrees of freedom, would give distinctive values for associations within each unit, and between members of each pair of units.

Kinship: As noted in the Introduction, it may sometimes be appropriate to consider the kinship between two animals as a structural variable influencing, likely positively, their probability of association. Kinship, as measured by relatedness, can be calculated if the genealogy of the population is known, but will more often be estimated using molecular genetic markers such as microsatellites (van de Casteele, Galbusera & Mattysen 2001). However, often kinship may most appropriately be considered as a factor influencing affiliation itself and therefore one would not want to factor it out before calculating affiliation, rather seeing how kinship relates to the output affiliations.

The relative significance of the different structural variables can be assessed in several ways. For instance, we can present standardized partial correlation coefficients of each predictor variable with the association index, controlling for the other predictor variables. Being dimensionless, these give easily-interpretable measures of the relative significance of the predictors. We can also carry out MRQAP tests for each predictor, controlling for the others. These can be the basis of stepwise procedures aimed at delineating an efficient subset of structural factors that affect association.

Using affiliation indices

With a few exceptions, generalized affiliation indices can be analyzed much as association indices. We can display them as a printed matrix, as a network diagram, or using multidimensional scaling or hierarchical cluster analysis (Whitehead 2008). We can examine the distribution of the generalized affiliation indices or network statistics derived from them, such as strength (gregariousness), connectedness and affinity (Croft, James & Krause 2008; Wey *et al.* 2008). We can see how these measures differ between classes of animal, such as the sexes, and how they may correlate with one another. We can look for fairly closed communities of affiliated individuals by techniques such as maximizing modularity (Newman 2006). We can use data-stream permutation tests to test null hypotheses that there is no real affiliation in the population (Bejder, Fletcher & Bräger 1998). For these tests, first the gregariousness values (if being used as a predictor), then the generalized affiliation indices, and finally the test statistic (e.g. the standard deviation of the indices) are recalculated after each permutation of the data. The value of the test statistic on the real data is compared with that for the permutations, giving a P-value.

Unlike association indices or counts of interaction, generalized affiliation indices can be negative. Thus, they cannot be used as input for principal coordinates analysis; further, some standard test statistics of permutation tests, such as the coefficient of variation of the indices, are inappropriate. (The standard deviation of the indices is an appropriate test statistic for both association and affiliation indices.) Negative generalized affiliation indices are also an issue when using network diagrams to illustrate the generalized affiliation indices. They can be omitted, or perhaps illustrated in a different way (different colour or line style) from the positive indices.

Evaluating generalized affiliation indices

Simulated data

We used simulated data to investigate to what extent the generalized affiliation indices produced by the method described above mirror input affiliations, and to examine whether the significance of the predictor variables suggested by the proposed method matched their input significance.

We constructed simulated data sets with the following characteristics: m individuals, each with a 50% probability of being male or female, s_i=0 or 1 respectively, a gregariousness, g_i, drawn from the uniform random distribution on [1 G]. There are n=m(m-1) dyads. Each dyad has a probability ρ of being designated a pair of "affiliates": f_{ij}=1 if i and j affiliates, f_{ij}=0 otherwise. Each pair of individuals may, or may not, associate during any of T sampling periods.

At the beginning of the simulation (sampling period 0), individuals have a 50% probability of being inside the study area. At the start of each sampling period individuals outside the study area have probability q of entering it, and those inside the study area probability of q of leaving, giving sequences: b_{it}=1 if individual i was in the study area in sampling period t, b_{it}=0 if not.

Then, for individuals i and j in sampling period t we define a propensity for association:

$$u_{ijt} = g_i \cdot g_j \cdot b_{it} \cdot b_{jt} \cdot (1+\sigma\cdot(s_i==s_j)) \cdot (1+ \phi \cdot f_{ij}) \quad (5)$$

This is dependent on the gregariousness of each individual (g_i, g_j), requires both to be in the study area during the sampling period (b_{it}=b_{jt}=1), and is increased if both are of the same sex (by a factor of 1+σ), or both are affiliates (by a factor of 1+ϕ). The probability that individuals i and j are associated in sampling period t is proportional to the propensity for association, u_{ijt}, with the constant of proportionality adjusted so that the maximum probability of association is a_{max}. This procedure then gives a record of

240 associated/not associated for each pair of individuals in each sampling period, from which we calculated
241 association indices as in equation 1.

242 Assuming that we knew the sexes of each individual, but not their actual gregariousness, actual
243 presence in the study area, or who were affiliates with whom, we estimated affiliation indices as
244 described above using the following predictors: sex similarity, estimated dyadic gregariousness
245 (equation 4), an estimate of temporal overlap (a simple ratio index using sets of five consecutive
246 sampling periods as the new long sampling period, and defining association as both animals identified in
247 a long sampling period), and a nuisance variable with uniform random numbers from the [0 1] interval
248 chosen for each dyad with no relationship to association. We used the linear model on the association
249 indices, the binomial model on the numerator and denominator of the association indices, and the
250 Poisson model just on the numerator of the association indices.

251 At the end of each run we retrieved the information on which pairs were affiliates, and compared the
252 association indices and affiliation indices of affiliated pairs and non-affiliated pairs. The success of an
253 index in identifying affiliates was indicated by Cohen's *d*, the difference between the mean of the index
254 for affiliated pairs and that for non-affiliated pairs divided by the pooled standard deviation.

255 For each data set we also calculated the partial correlation coefficient between the association indices
256 and each of the predictor variables, controlling for the other predictor variables. These partial
257 correlation coefficients were also the test statistic for MRQAP double semi-partialling (Dekker,
258 Krackhardt & Snijders 2007) tests for each predictor (null hypothesis that the predictor was linearly
259 unrelated to association, given the other predictors), with 1,000 replicates.

260 For each data set we tested for preferred/avoided associations using the 'permute associations within
261 sampling periods' methodology in which pairs of associates within sampling periods are flipped
262 maintaining the number of associates of each individual as well as the total number of associations

within each sampling period (Whitehead, Bejder & Ottensmeyer 2005). We tested both the association indices and generalized affiliation indices using this method (calculating generalized affiliation indices anew for each random data set), with 1,000 permutations and each permutation being made up of 1,000 flips. The null hypothesis of no preferred association/affiliation was rejected if the standard deviation of the real indices was greater than at least 950 of the standard deviations of the sets of random indices.

Initial runs were made using a "standard" set of parameters: n=20, G=2, T=50, ρ =0.09, q=0.1, σ=0.9, ϕ=2.0, a_{max}=0.6. In subsequent sets of runs, we changed the number of individuals (n=10, 40), number of sampling periods (T=25, 100), and mean rate of association (a_{max}=0.3, 0.85) to check the robustness of the results for smaller, larger, or differently-sampled data sets. Then we effectively removed any preference for affiliates (ϕ=0.0), gregariousness differences (G=1), and sex preferences (σ=0.0). In the final set of runs we increased the rates of movement into and out of the study area (q=0.4) effectively making our measure of temporal overlap (calculated over 5 consecutive sampling periods) no longer relevant. There were 100 runs with each set of parameters.

Bottlenose whale data

We used a data set on the social relationships of northern bottlenose whales (*Hyperoodon ampullatus*) based upon photoidentifications collected in three submarine canyons on the edge of the Scotian Shelf between 1988-2003, an extended version of the data set analyzed by Gowans et al. (2001). We used only those animals: a) with markings considered "reliable" allowing consistent matching between years; b) who could be allocated to age-sex classes as either mature males, subadult males or females based upon photographs of their foreheads; and c) who were identified on 15 or more different days (see Gowans, Whitehead & Hooker 2001). There were 16 animals in this data set. Sampling periods were days, and dyads were considered associated on a day if they were identified within 1 hour of each other.

We constructed half-weight indices between individuals using these data. We also calculated several predictor measures:

'Gregariousness': as in equation 4.

'Age-Sex': 1 if pair of same age-sex class; 0 otherwise.

'Temporal overlap': Proportion of years in which at least one of the individuals in the dyad was identified that both were identified.

'Spatial overlap': Proportion of those years in which both were identified, that both were identified in the same canyon.

We examined the significance of these predictor variables using MRQAP tests and partial correlation coefficients, sequentially removed predictors with non-significant (P>0.10) MRQAP tests, and then calculated generalized affiliation indices using a binomial model. We compared association and generalized affiliation indices for these whales using network diagrams, network statistics, as well as tests for age-sex class effects (Mantel tests) and overall affiliation (data-stream permutations).

Results

Simulated data

Results of the runs with simulated data are given in Supplemental Table 1.

For the first run with the standard set of parameters, network diagrams generated using the original simple ratio association indices as well as the generalized affiliation indices (binomial method) are shown in Fig. 1. When compared with the association indices, affiliation indices show true affiliations more prominently (red links are generally wider, and so less often dashed, on the lower, affiliation, diagram), are less affected by gregariousness (number of links less related to size of node in lower

diagram), and do not segregate genders (compare lower and upper diagrams). In Fig. 2 the distributions of association indices and affiliation indices (binomial, linear and Poisson) are compared for true affiliates and other dyads using box plots. The distinction between affiliated and non-affiliated dyads is much stronger—the boxplots are less overlapped—for all three types of affiliation index than for association indices. This difference was quantified using Cohen's *d*, with *d*=1.57 for association indices and *d*=2.30, 2.36 and 2.68 for binomial, linear and Poisson affiliation indices, respectively.

In all runs with simulated data, except those where affiliations were effectively disabled (ϕ=0), the affiliation indices better discriminated between affiliates and non-affiliates than association indices, with a mean increase in Cohen's *d* of 0.70, 0.62, and 0.98 for binomial, linear and Poisson runs respectively. When affiliations were effectively disabled (ϕ=0.0) the distinctions were virtually erased, with near zero values of Cohen's *d* for both associations and affiliations. The affiliation indices performed better with more sampling periods, and worse with a smaller population size, fewer sampling periods, and fewer associations.

The partial correlation coefficients and MRQAP tests clearly showed the irrelevance of the nuisance variable with near-zero partial correlation coefficients, and the null hypothesis of no relationship to association rejected in only about 5% of the runs, as expected. The analysis also clearly indicated the significance of the gender predictor variable, with strong partial correlation coefficients and universal rejection of the null hypothesis except when the gender similarity effect was removed (σ=0.0), when the partial correlation coefficient fell to nearly zero and the null hypothesis was rejected at the expected rate. The results were similar with the temporal predictor, although the partial correlation coefficient and null hypothesis rejection rate were not entirely reduced to zero by decoupling the migration rate from the length of the longer sampling periods. The most obvious discrepancy was for gregariousness

329 which was signalled as a useful predictor of association in many runs, including some of those in which
330 no gregariousness effect was input (G=1).

331 The permutation tests for preferred/avoided associations almost always rejected the null hypothesis of
332 no preferred/avoided associations for both the simple ratio indices and the generalized affiliation
333 indices. There were some failures to reject the null hypothesis with a population of only 10 individuals,
334 and with fewer associations (less dense network) for the generalized affiliation indices. The primary
335 distinction though is for the runs without built in affiliations (ϕ=0): the null hypothesis was generally
336 rejected when testing the simple ratio index, but not when testing the generalized affiliation index,
337 which had mean P-values of about 0.3. This shows that the generalized affiliation index had effectively
338 removed the non-affiliation sources of association, exposing cases when there was true affiliation
339 among individuals. Thus the generalized affiliation index fulfilled its mandate.

340 ## Bottlenose whale data

341 MRQAP tests indicated that age-sex class and temporal overlap were useful in explaining patterns of
342 association in the northern bottlenose whales (Table 1), with gregariousness and spatial overlap being
343 removed by the stepwise procedure. Using age-sex class and temporal overlap as predictors we
344 calculated generalized affiliation indices. Network diagrams of the association indices and generalized
345 affiliation indices are compared in Fig. 3. The primary distinction is that the network as portrayed by
346 half-weight indices is much more prominently structured by age-sex class than is the network of
347 generalized affiliation indices. The mature males appear to form a clique with their associations. The
348 network of generalized affiliation indices does not obviously show this characteristic, as might be
349 expected with age-sex class used as a structural factor in the calculation of the generalized affiliation
350 indices. However some strong relationships, for instance between mature males #1 and #3 are
351 maintained with the transformation into generalized affiliation indices.

352 We also compared several characteristics of the association indices to those of the generalized affiliation
353 indices (Table 2). In most respects the pattern of generalized affiliation indices appears less structured
354 than that of the half-weight association indices: there was less modularity, lower correlations between
355 strength (i.e. gregariousness for association indices) and other nodal network metrics, no support for
356 age-sex class structuring associations (versus a strong matrix correlation and significant Mantel test for
357 the same comparison with associations), and a permutation test did not reject the null hypothesis of no
358 preferred or avoided affiliations (versus a significant result for associations). However when the test just
359 included the 7 mature males, the test was marginally significant for generalized affiliation indices and
360 the original half-weight association indices (Table 2). (The structure of the data was not suitable for a
361 similar test of the 7 females.) Large deviance residuals (greater than 2.5) indicated two strongly
362 affiliated dyads: mature males #1 and #3 (2.81); subadult male #267 and female #102 (3.82). While the
363 relationship between #1 with #3 is clearly strong in the original association data (Fig. 3), that between
364 #267 and #102 had not been previously recognized as significant. There were no deviance residuals less
365 than -2.5 so little evidence for avoidance.

366

367 ## Discussion

368 Disinterring true affiliations from association or interaction data has been a major challenge in the study
369 of animal social networks (Bejder, Fletcher & Bräger 1998; Croft *et al.* 2011). In this paper we build on
370 the ideas of Godde et al. (2013) by removing structural predictors in the calculation of new indices that
371 reflect true affiliations (Fig. 4). The results of the evaluations of generalized affiliation indices with both
372 simulated and real data illustrate how the method can remove structural determinants of association,
373 leaving what appear to be fundamental affiliations that can be analyzed using a wide range of
374 techniques.

375 It is impossible to cover all potential scenarios with simulations, but from the consistency of the results
376 within the range that we covered, and the basic logic of the approach, we expect that within much or all
377 of the range of scenarios used to study animal societies generalized affiliation indices will provide
378 insight. Perhaps the most significant omission in our simulations are "gambit of the group" data, when
379 associations are defined by group membership (Whitehead 2008), and thus have extra dependencies.
380 Evaluating these scenarios is a next step.

381 Our methodology identifies affiliation using the residuals after removing structural predictors of
382 association. This definition-by-elimination is philosophically unsatisfactory, but avoiding it would need a
383 completely different approach. Practically it leads to two issues. The first is whether particular factors
384 should be included as structural predictors. Kinship could drive association directly or through
385 affiliation. Large-scale temporal use of the study area will usually be a structural factor, whereas small-
386 scale temporal patterns may be better considered elements of affiliation. In cases of uncertainty, we
387 suggest calculating the generalized affiliation indices with and without the ambiguous factor.

388 The second issue deriving from our negative connotation of affiliation constitutes the primary limitation
389 of the technique: it can only be only as effective at removing structural determinants of association as
390 these determinants are represented by the predictor variables entered into the model. Structural non-
391 affiliative factors that affect association but are not represented by the predictor variables will remain.
392 Our simulations suggested that even imperfect predictor variables (such as the temporal overlap
393 predictor used for our simulated data sets) can do a good job of exposing true affiliations. Predictors
394 can also fill in for one another, and mask each other. For instance, the gregariousness predictor includes
395 how available individuals are to observation. This, we think, is why gregariousness was sometimes found
396 to be a useful predictor in our simulations even when input gregariousness was disabled (G=1). Our

measure of gregariousness was covering some of the variation in association rates produced by different individual use of the study area.

Another concern is when predictor variables are calculated from the association data. For this reason, we used a "jackknife" definition of gregariousness (equation 4). A similar problem of circularity, and potential resultant loss of power for generalized affiliation indices as indicators of true affiliation, arises if memberships of social units are used as predictor variables (see above) when these social units are themselves delineated from the association data using cluster analysis or maximization of modularity.

The model that we have postulated (equation 2) assumes additivity of predictor variables. So, for instance, the range overlap effect is added to the gregariousness effect to produce an expected value of the association index. In some situations multiplicative effects may be more appropriate, so that if there is little range overlap between a pair, the possible effect of their similarity in gregariousness is proportionally reduced. This could be achieved by logging the structural variables (as in our definition of gregariousness, equation 4), and possibly changing the link function. However using an additive model (equation 2) on our simulated data which were produced using a multiplicative model (equation 5), seemed to work effectively.

In their quest to control the structural factors affecting association, current data stream permutation tests—that of Bejder et al. (1998) and its successors—are quite complex and time consuming. As the generalized affiliation index specifically removes the effects of the structural factors, performing the data stream permutation tests on the generalized affiliation indices seems overkill—the structural factors are apparently being removed twice. Simpler node-permutations of the data in each sampling period do not work, as predictor variables, such as spatial overlap, no longer match the data. Using our random data, we have explored the possibility of using the fit of the binomial generalized linear model (indicated by deviance) to the association data as a test for underlying affiliations. If there are no

420 affiliations then the binomial model should fit. Although, in our explorations, this method had high Type
421 I error rates, there may be other relatively-simple ways to test for underlying affiliations in a social
422 network using generalized affiliation indices. It would also be very useful good to have an overall "effect
423 size" for the degree of affiliation in the population. The social differentiation (estimated coefficient of
424 variation of true association indices, before sampling) attempts this for association indices (Whitehead
425 2008), but much more useful would be a counterpart for affiliation indices.

426 The technique that we have explored could easily be extended in a variety of ways. It could be used on
427 interaction counts (perhaps using the Poisson version of the generalized linear model) or rates (perhaps
428 using time spent observing each dyad as an offset predictor variable). It could be used on asymmetric
429 data (e.g. grooming), and on rectangular rather than square association matrices (e.g. males versus
430 females). Categorical variables (a category for each dyad) could be used as predictors.

431 One of us (HW) has incorporated the calculation and analysis of generalized affiliation indices, including
432 all the features used in our examples, into the next (soon to be released) version of SOCPROG, a
433 MATLAB-based package for the analysis of animal social structure (Whitehead 2009). Other social
434 analysis packages, such as the R program asnipe (Farine 2013), might be integrated with this
435 methodology, or extended to use it directly.

436 Conclusion

437 Generalized affiliation indices provide a new route for uncovering affiliations in animal social networks.
438 They can be used instead of structured data-stream permutation tests, or in conjunction with them.
439 They are more flexible than currently available data-stream permutation tests in how they deal with
440 structural factors affecting association, and can be used for a wide range of purposes, including the
441 production of affiliation-based network diagrams, network statistics, division into communities, and
442 testing for overall affiliation.

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Data Accessibility

In the supporting information are:

Data_scripts.pdf: Explains script and data files

MATLAB_scripts.zip: MATLAB scripts producing and analyzing random data

SOCPROG2.6.zip: files for the latest draft, unreleased, version of SOCPROG (including generalized affiliation indices), as well as SOCPROG files with the northern bottlenose whale data.

Table_S1.pdf: Results of simulation analysis

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508

509 Table 1. Efficiency of predictor variables in explaining association indices among bottlenose whales, as
510 shown by partial correlation coefficients and results of MRQAP tests (1,000 replications).

511

Predictor	Partial correlation	MRQAP P-value
Gregariousness	0.068	0.300
Age-sex	0.292	0.001
Temporal overlap	0.295	0.002
Spatial overlap	0.117	0.109

512

513

514 Table 2. Statistics and tests of half-weight association indices and generalized affiliation indices for 16

515 northern bottlenose whales.

	Association indices	Generalized affiliation indices
Differences between age-sex classes:		
Matrix correlation	0.413	0.008
Mantel test, P-value (1,000 permutations)	0.000	0.569
Correlation coefficients among network statistics[1]:		
Strength by clustering coefficient	0.653	0.077
Strength by affinity	0.710	0.030
Modularity[2]:		
Communities identified using modularity	2	4
Modularity	0.235	0.112
Tests for preferred associations[3]		
All whales (*n*=16)		
sd (indices), real : random (mean)	0.094 : 0.090	0.079 : 0.079
P-value	0.002	0.439
Mature males (*n*=7)		
sd (indices), real : random (mean)	0.132 : 0.125	0.124 : 0.117
P-value	0.094	0.082

516 [1]Network statistics are: strength (sum of association indices or generalized affiliation indices linking each

517 individual); clustering coefficient (a measure of how well the associates of an individual are themselves

associated using the matrix definition of clustering coefficient for weighted networks of Holme et al. (2007)); affinity (the strength of an individual's associates, weighted by the association index between the individual and each of them).

[2]Modularity indicates how well a network can be divided into communities. We use Newman`s (2006) eigenvector-based method. Modularities above 0.3 indicate substantial support for the division (Newman 2004).

[3]Permutation tests using flips of pairs of associations within sampling periods with 1,000 permutations, 1,000 flips/permutation (Whitehead 2008, 129-130). Test not possible just using females because of data structure.

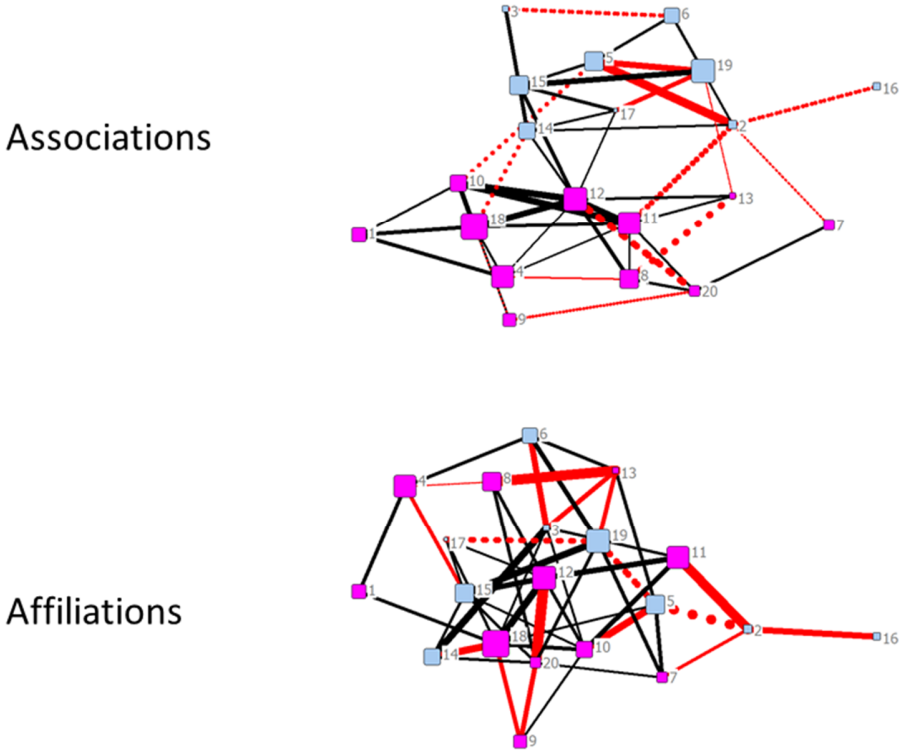


Figure 1

Network diagrams using one run of simulated data (for parameters, see main text), using association indices (above) and generalized affiliation indices (below). Arrangements are optimized using the default spring-embedding algorithm of NetDraw. The colour of each node indicates its gender, size its gregariousness. Only links representing indices in the upper 25% percentile are shown, and link width is proportional to index weight. Input dyadic affiliations are shown by red links. When the standardized (mean 0; SD 1) association indices are greater than the standardized generalized affiliation indices for dyadic affiliations, the red links are dotted in the lower diagram, and when the standardized generalized

537 affiliation indice are larger than the standardized association indicess, the red links are dotted in the

538 upper diagram.

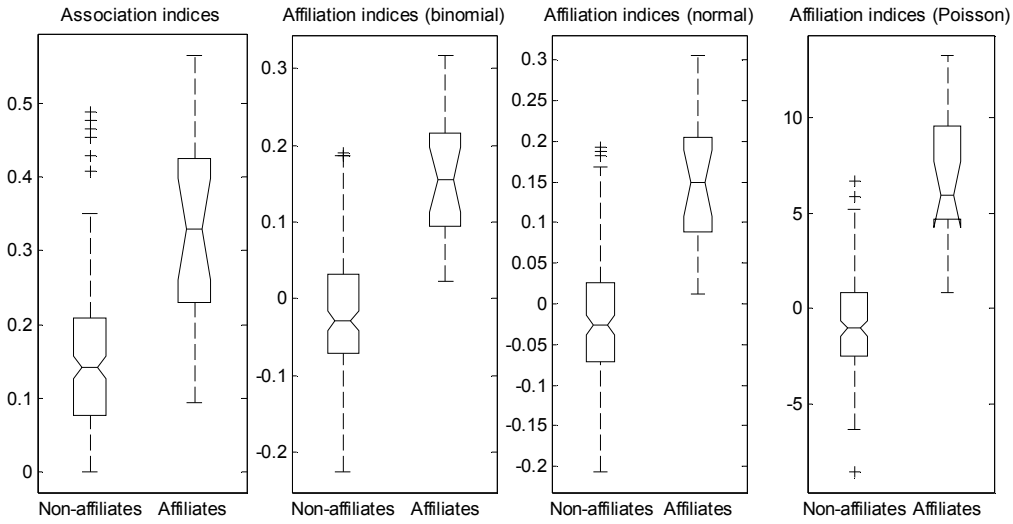
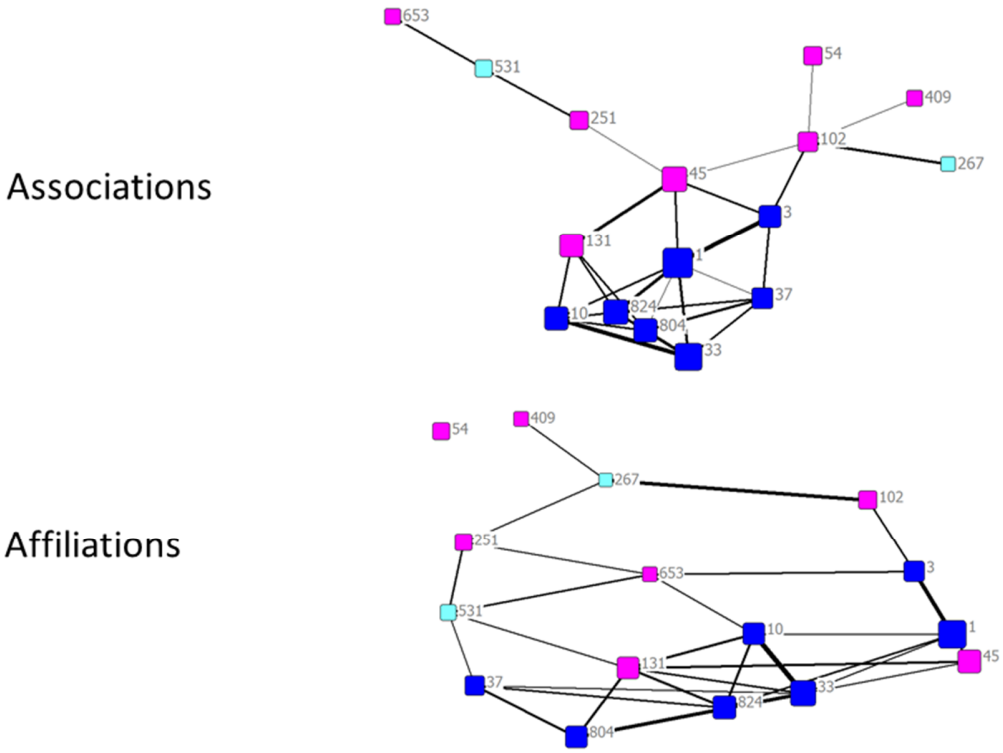


Figure 2

Boxplots comparing the distribution of association and (binomial, linear, Poisson) generalized affiliation indices for true affiliates and non-affiliates using the same simulated data that produced the network diagrams in Figure 1.

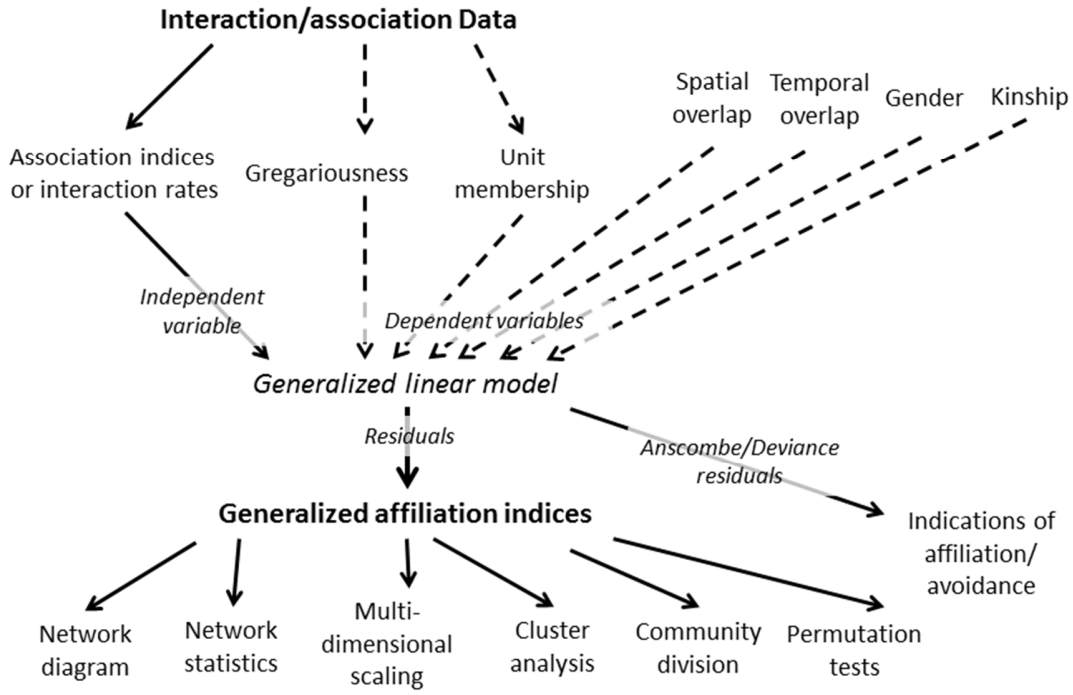


547
548 **Figure 3**

549 Network diagrams for 16 northern bottlenose whales using association indices (above) and generalized
550 affiliation indices (below). The colour of each node indicates its age-sex class (pink females; dark blue
551 mature males; light blue subadult males), the size of each node its gregariousness. Other attributes as in
552 Figure 1.

553

554



555

556 **Figure 4**

557 The construction and usage of generalized affiliation indices.